Q11.U55
3328

PROCEEDINGS OF THE UNITED STATES NATIONAL MUSEUM

APR 1954
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

Issued *by the*

SMITHSONIAN INSTITUTION
U. S. NATIONAL MUSEUM

Vol. 103 Washington: 1954 No. 3328

REVIEW OF THE ATLANTIC PERIWINKLES, NODILITTORINA, ECHININUS, AND TECTARIUS

By R. Tucker Abbott

Since the 1942 publication in Johnsonia of "The Genera *Tectarius* and *Echininus* in the Western Atlantic" by Clench and Abbott, enough additional data have been assembled to warrant a review of this group of tropical, littoral snails. In addition to the anatomical, distributional, and biological information presented here, there is a short discussion of the phylogenetic position of the genus *Echininus*, and some changes in nomenclature.

It had been noted for some time that the operculum of *Echininus* was multispiral, a feature commonly found among members of such families as the Trochidae, Potamididae, and Modulidae but unusual for the Littorinidae, which are well known for their paucispiral opercula. In a paper that has generally been overlooked, Kesteven (1903) removed the genus *Echininus* (*Echinella* of Kesteven) from its customary position in the Littorinidae and placed it in the Modulidae. This has necessitated our making a study of the gross anatomy of *Echininus*, *Tectarius*, and *Modulus*. This study was made possible through the generosity of Mrs. Germaine L. Warmke, who collected and airmailed living specimens of *Echininus nodulosus* Pfeiffer and *Nodilittorina tuberculata* Menke from Puerto Rico. In the process of comparing the latter species with *Tectarius muricatus* Linné, we came to the conclusion that *Nodilittorina* should be considered as a full genus closely related to *Melarhaphe* or *Littoraria* rather than as a subgenus of *Tectarius*.

The nomenclatorial adjustments in this paper involve changing the name used in Johnsonia, *Tectarius tuberculatus* Wood, to *Nodilittorina tuberculata* Menke, and a new and presumably valid genotype designation for *Nodilittorina*.

Family Littorinidae

Genus *Nodilittorina* von Martens, 1897

In Johnsonia, Clench and I had erroneously considered *Nodilittorina* as a subgenus of *Tectarius*. From a study of the shell and animal characters, the radula, and the type of egg capsules, it appears that this group is much more closely allied to the *Melarhaphe* or *Littoraria* subgenera of *Littorina* than to *Tectarius*. An obvious relationship in shell characters is seen between the Indo-Pacific *Melarhaphe mauritiana* Lamarck and such *Nodilittorina* as *miliaris* Quoy and Gaimard and *picta* Philippi, all of which have the peculiarly flattened, thin inner columella edge and the axial, zigzag color streaks on the whorls. The latter two, *miliaris* and *picta*, have strong sculpturing which tends towards the production of small nodules which are characteristic of *Nodilittorina*.

The floating egg capsule of *Nodilittorina tuberculata* Menke and *Littorina* (*Melarhaphe*) *ziczac* Gmelin (copied in our fig. 55 from Marie Lebour, 1945) are similar in that they are drum-shaped and with 6 to 7 spiral lines or ridges on the top surface. These spiral ridges are absent in the capsules of *Tectarius muricatus* Linné and *Littorina* (*Melarhaphe*) *neritoides* Linné. The latter species is from the eastern Atlantic and is the genotype of *Melarhaphe*. Should it prove to have a simple, single-pronged penis, as does *Tectarius*, it is likely that such species as *L. ziczac* Gmelin and *L. mauritiana* Lamarck (which have complicated, *Nodilittorina*-like penes) do not belong to *Melarhaphe*, sensu stricto.

Three recent papers have contributed to our knowledge of littorinid egg capsules (Ostergaard, 1950; Tokioka, 1950; and Tokioka and Habe, 1953.) There appear to be three groups of capsules: (1) Helmet-shaped—*Littorina littorea* Linné (Lebour, 1935, p. 375) and *Littorina pinctado* Wood (Ostergaard, 1950, p. 97); (2) simple drum-shaped—*Littorina neritoides* Linné (Lebour, 1935, p. 375) and *Tectarius muricatus* Linné (Lebour, 1945, p. 465); and (3) drum-shaped, with ridges on the top surface—*Littorina ziczac* Gmelin (Lebour, 1945, p. 465) and *Nodilittorina tuberculata* Menke (Lebour, 1945, p. 465).

To the latter group, Tokioka and Habe add the egg capsules of three possible littorinid snails. These capsules were given the non-binomial names of "*Littorina-capsula habei, multistriata,* and *hagruma.*" The Japanese capsules differ from those in the Western Atlantic species in having concentric instead of spiral ridges on the top surface. The "*hagruma*" capsule is unique in bearing on its peripheral surface a series of 21 gearlike undulations.

The genus *Hamus* of Klein seems to have been first validated in 1886 by R. B. Watson (Scaphopoda and Gasteropoda, *in* Report on the Scientific Results of the Voyage of HMS *Challenger* . . . , vol. 15, pt. 42, p. 576). Although he intended it for the group we know as *Nodilittorina*, I prefer to relegate *Hamus* to the synonymy of the trochid *Turcica* A. Adams, 1854, by here designating *Tectaria montrouzieri* Fischer, 1878, as the genotype of *Hamus* Watson, 1886. For identity of that trochid species see Hedley (1901, p. 121).

Wenz's (1939, p. 523) genotype designation of *Nodilittorina* is invalid, since *Turbo nodulosus* Gmelin is not one of the species included by von Martens in 1897 either in name or substance and since *Turbo* (not *Trochus*) *nodulosus* Gmelin is a turbinid species. Von Marten's *Littorina nodulosa* Pfeiffer is an *Echininus*. I hereby designate *Littorina pyramidalis* Quoy and Gaimard as the genotype of *Nodilittorina* von Martens, 1897. This species is *Trochus nodulosus* Gmelin, non Solander, 1766.

Habe (1951, p. 90) followed the error of Clench and Abbott (1942) in considering *Turbo tuberculata* Wood the same as Gmelin's *nodulosus*. Actually it is the West Indian *Echininus*, as seen by our revised synonymy. *Littorina tuberculata* Wood is not included by name in von Martens' genus and cannot be designated as the genotype.

Below, I have included a revised synonymy of the Western Atlantic *Nodilittorina tuberculata* Menke which Clench and I had erroneously listed in Johnsonia as *Tectarius tuberculatus* Wood. Our error arose in not recognizing Wood's figure as representing the Atlantic *Echininus*. Although the columella region of the shell illustrated by Wood is very close to that found in some *Nodilittorina*, the nature and number of nodules clearly identifies it as *Echininus nodulosus* Pfeiffer.

***Nodilittorina tuberculata* Menke**

Trochus nodulosus Gmelin (non Solander, 1766), Caroli a Linné Systema naturae . . . , ed. 13, p. 3582, No. 98, 1791 (in part as variety minor). (Mari, Americam meridonalem.)

Litorina tuberculatus Menke, Synopsis methodica Molluscorum . . . , p. 25 (Pyrmonti), 1828 (refers to Gmelin's minor).

Litorina thiarella Anton, Verzeichniss der Conchylien . . . , p. 53, 1839.

Littorina nodulosa d'Orbigny, Mollusques, vol. 1, p. 205 (exclusive of synonymy), pl. 14, figs. 11–14, *in* de la Sagra, Histoire physique, politique et naturelle de l'Ile de Cuba, 1841. (Cuba, Martinique, and St. Lucia.)

Littorina dilatata d'Orbigny, Mollusques, vol. 1, p. 207, pl. 14, figs. 20–23, *in* de la Sagra, Histoire . . . naturelle . . . de Cuba, 1841. (Havana.)

Shell.—It is easy to confuse this species with *Echininus nodulosus* Pfeiffer, especially since their ranges overlap and their habitats are almost identical. *N. tuberculata* is usually 4 mm. to 5 mm. smaller than *E. nodulosus* from the same small area. The nodules in each

spiral row on the periphery of the whorl are always lined up under one another in *N. tuberculata*, while in *E. nodulosus* they are not, since the upper row bears fewer (and larger) nodules than the lower row.

Sexual dimorphism in the form of shell length was very slight in 103 specimens examined from Rincon Lighthouse, Puerto Rico. Of that number, 38 percent were males; their mean shell length was 7.7 mm. The mean length of the females was 9.1 mm. In *Echininus* the difference in the sizes of the shells of the two sexes was more pronounced, but this is a feature which is variable from colony to colony in the same species (see Abbott, 1949).

Animal.—Live specimens from Rincon Lighthouse, western Puerto Rico, were examined. The animal is typically littorinid. The tentacles are translucent yellowish with a small, circular band or ring of black around the region near the distal end. The underside of the foot is yellowish to yellowish gray with a distinct, longitudinal, indented line dividing the foot into two lateral areas. The furrow is more prominent near the center, and disappears towards the posterior and anterior ends of the sole. The waves of progression are retrograde and ditaxic (see Vlès, 1907, and remarks under *Tectarius muricatus*). The foot progresses somewhat in the manner of a person slowly shuffling forward in a potato sack.

The penis is large and located on the right side of the body under the base of the right tentacle. On the anterior edge of the penis there is a large, bean-shaped, snow-white gland, and just distal to it is a short, fairly large, clear accessory flagellum. The main prong of the penis is slender and tapering to a point, with a nearly closed seminal groove along the posterior edge. The penis of *N. tuberculata* is very similar to that of preserved specimens I have examined in *Littorina* (*Melarhaphe*) *ziczac* Gmelin from the Bahamas.

Radula.—The ribbon is very long with the unused part coiled up like a watch spring in a pocket in the dorsal region behind the head. One specimen from Puerto Rico had about 1,125 transverse rows. The ribbon is delicate and half as wide as that found in *Echininus*. The central tooth is narrow, with the appearance of having been laterally compressed. It bears a large central cusp, and, crowded over this, are the two lateral cusps. The lateral and inner marginal teeth are massive, each with a large inner cusp and a much smaller outer cusp. The outer marginal tooth is smaller, fairly weak; it bears 5 denticles in Puerto Rico specimens and 8 denticles in Habana, Cuba, specimens.

Parasitology.—In living specimens examined from the rocky shore near Habana, Cuba, several specimens of *N. tuberculata* were found to be heavily infected with single-tailed, two-eye-spotted cercariae whose

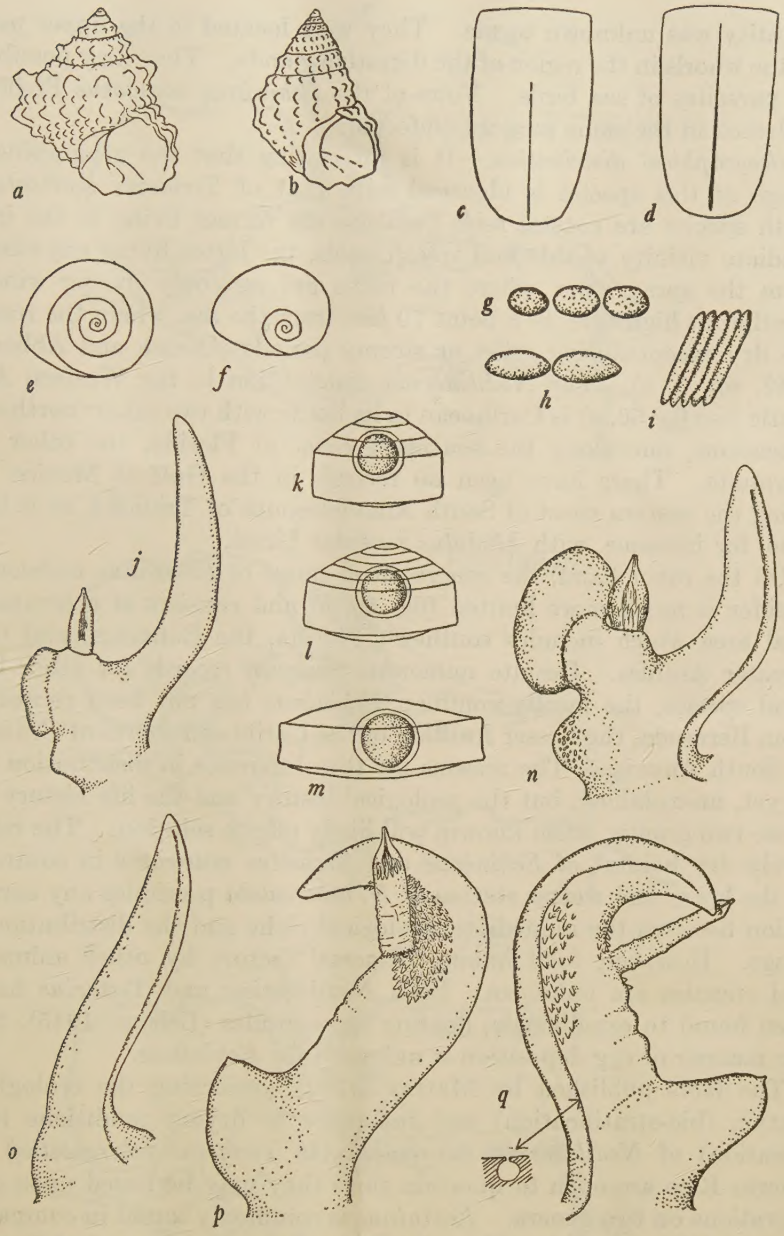

FIGURE 55.—*a*, Shell of *Echininus nodulosus* Pfeiffer (× 1½). *b*, Shell of *Nodilittorina tuberculata* Menke (× 1½). *c*, Underside of foot of *E. nodulosus* (× 2). *d*, Underside of foot of *N. tuberculata* (× 2). *e*, Operculum of *E. nodulosus* (× 2). *f*, Operculum of *N. tuberculata* (× 2). *g*, Fecal pellets of *E. nodulosus* (× 4). *h*, Fecal pellets of *N. tuberculata* (× 4). *i*, Fecal pellets of *Modulus modulus* Linné (× 4). *j*, Penis of *Littorina ziczac* Gmelin (× 6). *k*, Floating egg capsule of *L. ziczac* (diam. 0.20 mm.). *l*, Egg capsule of *N. tuberculata* (diam. 0.24 mm.). *m*, Egg capsule of *Tectarius muricatus* Linné (diam. 0.24 to 0.32. After Lebour, 1945). *n*, Penis of *N. tuberculata* (× 6). *o*, Penis of *T. muricatus* (× 6). *p*, *q*, Penis of *E. nodulosus* (× 6).

identity was unknown to me. They were located in the upper part of the whorls in the region of the digestive glands. They may possibly be parasites of sea birds. None of the *Echininus nodulosus* Pfeiffer collected in the same area was infected.

Geographical distribution.—It is interesting that the geographical range of this species is identical with that of *Tectarius muricatus*. Both species are coastal rock dwellers, the former living in the immediate vicinity of tide and splash pools, the latter living anywhere from the spray zone, where the rocks are wet only during windy weather at high tide, to a point 70 feet from the sea, where the rocks are dry except during rainy or stormy periods (Clench and Abbott, 1942, pp. 2, 3). The *Nodilittorina* distribution in the Western Atlantic (see fig. 56, *a*) is Caribbean in its limits with two minor northern extensions, one along the southeast coast of Florida, the other in Bermuda. There have been no records in the Gulf of Mexico or along the eastern coast of South America south of Trinidad, as is the case, for instance, with *Modulus modulus* Linné.

On the other hand, the geographical range of *Echininus nodulosus* Pfeiffer is much more limited (fig. 56, *b*) and consists of a compact oval area which includes southeast Florida, the Bahamas, and the Greater Antilles. Despite numerous museum records for other littoral species, the locally common *Echininus* has not been recorded from Bermuda, the Lesser Antilles, or the Caribbean shores of Central or South America. The reasons for this difference in distribution is, as yet, unexplained, but the geological history and the life history of these two groups, when known, will likely offer a solution. The relatively dry habitat of *Echininus* and *Tectarius muricatus* in contrast to the lower and wetter station of *N. tuberculata* precludes any correlation between the immediate, ecological niche and the distributional range. However, food habits, dispersal factors by other animals, and enemies are unknown. Both *Nodilittorina* and *Tectarius* have been found to expel single, floating egg capsules (Lebour, 1945), but the manner of egg deposition is unknown for *Echininus*.

The facts published by Mattox (1949) concerning the ecological station (bio-stratification) and resistance to drying conditions (exsiccation) of *Nodilittorina tuberculata* (as *Tectarius tuberculatus*) in Puerto Rico are open to question since they may be based upon observations on two genera. *Echininus* is commonly found in company with *Nodilittorina* along the rocky shore of the western end of Puerto Rico. The two are easily confused and the author makes no mention of the common *Echininus* in his report on the eight littoral species of that area.

New records.—Bahamas: Andros Island; Aklin Island; New Providence Island; Great and Little Inagua Islands; Mariguana

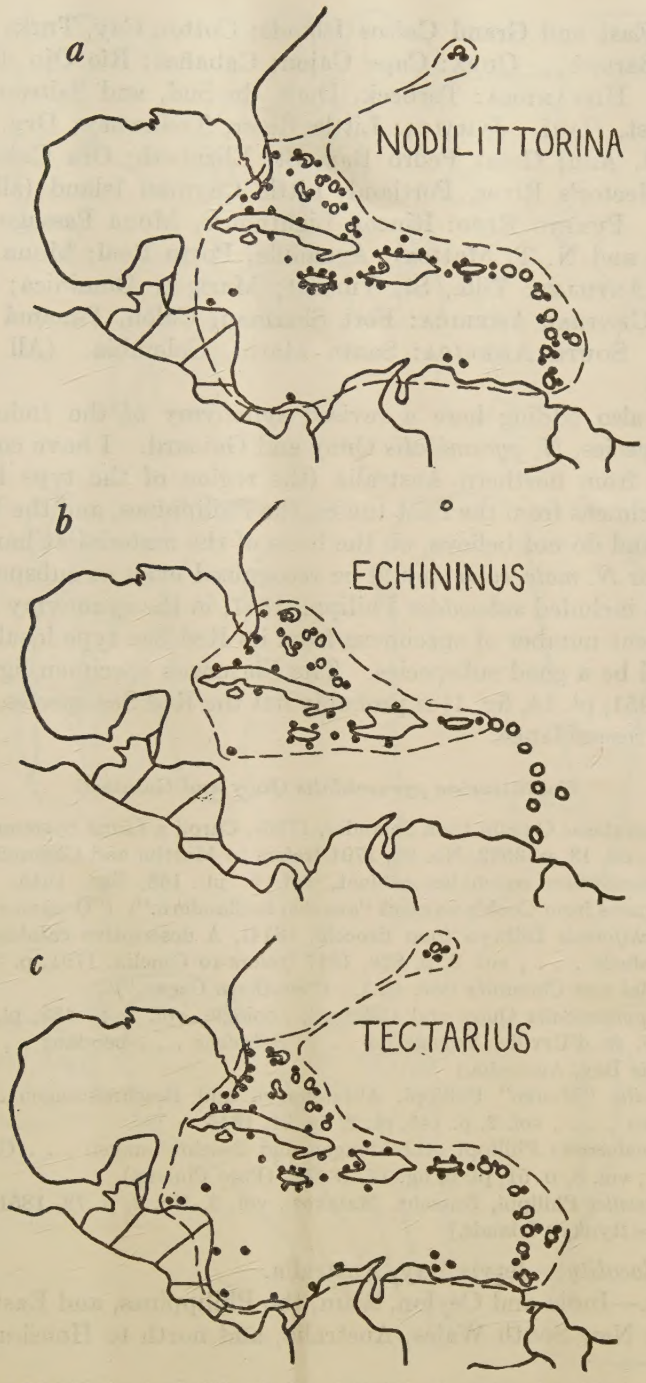

FIGURE 56.—Distribution in the West Indies of *Nodilittorina tuberculata* Menke, *Echininus nodulosus* Pfeiffer and *Tectarius muricatus* Linné (see locality records in text).

Island; East and Grand Caicos Islands; Cotton Cay, Turks Islands (all P. Bartsch). CUBA: Cape Cajon; Cabañas; Río Ojo de Toro, Oriente. HISPANIOLA: Torbeck, Dept. du Sud, and Saltrou, Dept. de l'Ouest, Haiti. JAMAICA: Little River, Trelawney; Dry Harbor Cave, St. Ann; Great Pedro Bay, St. Elizabeth; Ora Cabesa, St. Mary; Hector's River, Portland; Little Cayman Island (all C. R. Orcutt). PUERTO RICO: Rincon Lighthouse, Mona Passage (G. L. Warmke and N. T. Mattox); Aguadilla, Porto Real; Mona Island. LESSER ANTILLES: Villa, St. Vincent; Marigot, Dominica; Guadeloupe. CENTRAL AMERICA: Fort Sherman, Colón, Panamá (L. D. Sayers). SOUTH AMERICA: Santa Marta, Colombia. (All records USNM.)

I am also adding here a revised synonymy of the Indo-Pacific sibling species, *N. pyramidalis* Quoy and Gainard. I have compared material from northern Australia (the region of the type locality) with specimens from the East Indies, the Philippines, and the Ryukyu Islands and do not believe, on the basis of the material at hand, that *N. vilis* or *N. malaccana* should be recognized even as subspecies. I have not included *subnodosa* Philippi, 1847, in the synonymy for lack of sufficient number of specimens from its Red Sea type locality. It may well be a good subspecies. The Formosan specimen figured by Habe (1951, pl. 14, fig. 1) is probably not the Red Sea species, despite its close resemblance.

***Nodilittorina pyramidalis* Quoy and Gaimard**

Trochus nodulosus Gmelin (non Solander, 1766), Caroli a Linné Systema naturae . . . , ed. 13, p. 3582, No. 98, 1791 (refers to Martini and Chemnitz, Neues Systematisches conchylien-cabinet, vol. 5, pl. 168, figs. 1545, 1546 (of specimens from Cook's voyages "aus den Sudlandern.") ("Öceano australi.")

Turbo trochiformis Dillwyn (non Brocchi, 1814), A descriptive catalogue of recent shells . . . , vol. 2, p. 826, 1817 (refers to Gmelin, 1791, p. 3582, and Martini and Chemnitz (loc. cit.). ("Southern Ocean.")

Littorina pyramidalis Quoy and Gaimard, Zoologie, vol. 2, p. 482, pl. 33, figs. 12–15, *in* d'Urville, Voyage de . . . l'*Astrolabe* . . . pendant . . . , 1833. (Jervis Bay, Australia.)

Litorina vilis "Menke" Philippi, Abbildungen und Beschreibungen . . . Conchylien . . . , vol. 2, p. 145, pl. 2, fig. 21, 1846.

Litorina malaccana Philippi, Abbildungen und Beschreibungen . . . Conchylien . . . , vol. 3, p. 51, pl. 6, fig. 17, 1847. (Pulo Pinang.)

Litorina cecillei Philippi, Zeitschr. Malakoz., vol. 8, No. 2, p. 78, 1851. (Liewkiew=Ryukyu Islands.)

Type locality.—Jervis Bay, Australia.

Range.—India and Ceylon, Siam, the Philippines, and East Indies, south to New South Wales, Australia, and north to Honshu, Japan.

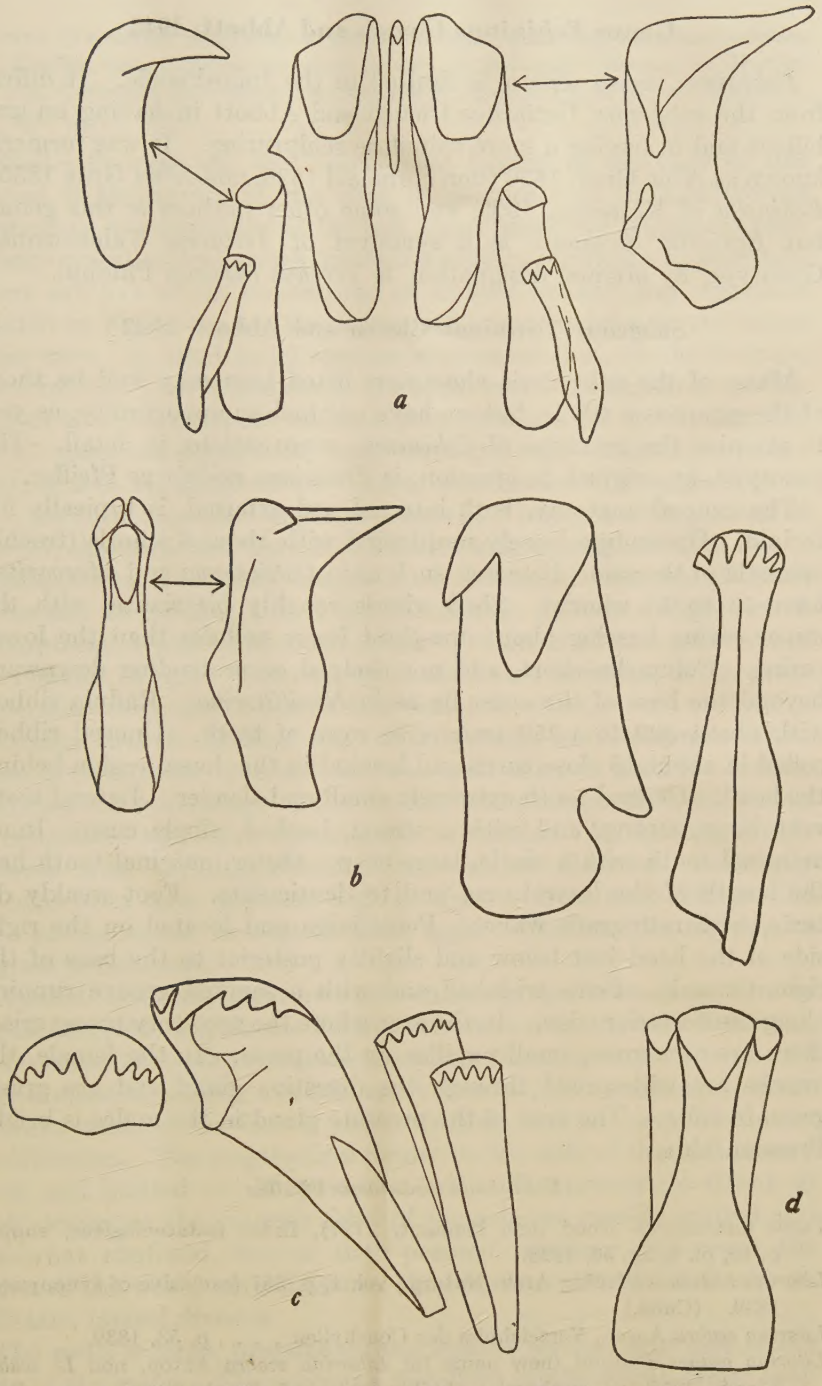

FIGURE 57.—Radulae of, *a*, *Echininus nodulosus* Pfeiffer, *b*, *Nodilittorina tuberculata* Menke, *c*, *Modulus modulus* Linné, and, *d*, the central tooth of *Tectarius muricatus* Linné. (Arrows point to side views of teeth.)

Genus *Echininus* Clench and Abbott, 1942

Echininus, sensu stricto, is limited to the Indo-Pacific. It differs from the subgenus *Tectininus* Clench and Abbott in having an umbilicus and in having a more spinulose sculpturing. It was formerly known as *Nina* Gray, 1850 (non Horsfield 1829, non *Nina* Gray 1855). *Echinella* of Kesteven, 1903, and some other authors is this genus, but *Echinella* Swainson is a synonym of *Tectarius* Valenciennes. Genotype, by original designation, is *Trochus cumingi* Philippi.

Subgenus *Tectininus* Clench and Abbott, 1942

Many of the subgeneric characters listed here may well be those of the genus as a whole, but we have not had an opportunity, as yet, to examine the genotype of *Echininus*, sensu stricto, in detail. The genotype, by original designation, is *Echininus nodulosus* Pfeiffer.

The general anatomy, both internal and external, is typically littorinid. Operculum loosely multispiral with about 6 whorls (trochid opercula of the same diameter, such as in *Calliostoma* and *Margarites*, have 11 to 13 whorls). Shell whorls roughly bicarinate, with the upper carina bearing about one-third fewer nodules than the lower carina. Columella short, and not shelved or protruding downward beyond the base of the outer lip as in *Nodilittorina*. Radula ribbon with about 800 to 1,250 transverse rows of teeth. Unused ribbon coiled in about 16 close turns and located in the dorsal region behind the head. Central tooth extremely small and slender. Lateral teeth very large, strong, and with a strong, hooked, single cusp. Inner marginal tooth with a single, large cusp. Outer marginal tooth half the length of the lateral one, and tri-denticulate. Foot weakly ditaxic, with retrograde waves. Penis large and located on the right side of the head just below and slightly posterior to the base of the right tentacle. Penis tri-lobed and with a seminal groove running along the posterior edge. In the area where the accessory prong arises there are numerous, small papillae on the penis. In the female, the ovaries are widespread through the digestive gland and are grass-green in color. The area of the prostate gland in the males is bright Prussian blue.

Echininus nodulosus Pfeiffer

Turbo tuberculatus Wood (non Pennant, 1777), Index testaceologicus, suppl., p. 19, pl. 6, fig. 30, 1828.

Litorina nodulosa Pfeiffer, Arch. Naturg., vol. 1, p. 357 (exclusive of synonymy), 1839. (Cuba.)

Litorina scabra Anton, Verzeichniss der Conchylien . . . , p. 53, 1839.

Litorina antoni Philippi (new name for *Littorina scabra* Anton, non *L. scabra* Linné, 1758, of authors), Abbildungen und Beschreibungen . . . Conchylien . . . , vol. 2, p. 145, pl. 2, fig. 18, 1847.

Litorina (*Tectarius*) *pfeifferianus* Weinkauff (new name for *Littorina nodulosa* Pfeiffer, non *Littorina nodulosa* Gmelin of authors), *Litorina*, *in* Martini and Chemnitz, Systematisches Conchylien-Cabinet, vol. 2, pt. 9, p. 46, pl. 5, figs. 15, 16, 1882.

Shell.—Perhaps the most distinctive feature of the shell of this species is the nature of the rows of nodules. As in *Nodilittorina tuberculata*, the periphery of the last whorl bears two prominent rows of large nodules, thus giving the shell a slightly bicarinate appearance. There are five or six minor rows of smaller beads. But especially notable in *Echininus* are the fewer and larger nodules in the upper major row. A count in 30 specimens revealed that, on the average, there are 3 or 4 fewer nodules in the upper row. No significant difference in this feature could be found between the males and the females. (In 15 males, the upper row, on the average, bore 11.3 nodules with a range of 9 to 14; the lower row had 14.9 nodules with a range of 11 to 17. In 15 females, the upper row bore 10.9 nodules with a range of 9 to 13; the lower row bore 13.0 nodules with a range of 10 to 15.)

Measurements of shell length were compared between 18 adult males and 21 females, and it was found that there is a slight sexual dimorphism in which the mean length of males is 13 mm. and that of the females 15 mm. The overlap in shell size, however, is too great to permit distinction of sex on this character alone.

I notice that the shells of some of the females are more eroded than those of the males, and in this connection there is need for further study on the wanderings of the females and their possible subjection to conditions slightly different from the males. M. Lebour (1945) believes that the amphibious Littorinids of Bermuda seasonally descend from their positions high in trees or from rock cliffs to the edge of the ocean to deposit their eggs. Whether the males also migrate is unknown.

Animal.—Our studies were made on living specimens from Rincon Lighthouse, western Puerto Rico. The animal is typically littorinid, as discussed under the remarks concerning the subgenus. The mantle edge is smooth, slightly swollen, and yellowish; the remainder is clear. The underside of the foot is yellowish gray, but not as yellow as in *Nodilittorina*. The longitudinal fissure on the sole of the foot is very weak and limited to the posterior half. The retrograde (front to back) waves at the anterior third of the sole are usually several and somewhat confused, but as they proceed posterior and reach the region of the weak, central fissure, they become stronger and take on a ditaxic, lateral division.

The penis is large, prominent, and located on the right side of the body of the males. The accessory flagellum is cylindrical, larger than that found in *Nodilittorina*, and located one-third from the distal end

of the penis. On both sides of the penis, in the region near the accessory flagellum, the surface bears numerous, small, fleshy, opaque-white papillae. These are absent in *Nodilittorina* and *Tectarius muricatus*. The posterior edge of the penis bears a narrow, nearly sealed seminal groove which ends near the distal end of the penis, and which has its origin on the side of the body some 2 mm. from the base of the penis. The region of the prostate gland on the right border of the mantle is cobalt blue in color. In mature females, this region bears the swollen, elongate, opaque-white accessory gland.

Radula.—The radula of *Echininus nodulosus* Pfeiffer (fig. 57, *a*) is very distinctive, although it conforms in general pattern to those found in the family Littorinidae. The reduction of the central tooth is most remarkable in that it has become a short, thin, sliverlike tooth. The main function of rasping has been taken over by the greatly enlarged, coarse lateral teeth. The inner and especially the outer marginal teeth are somewhat reduced. The tendency to reduce the central tooth appears to be a development arising perhaps through the *Nodilittorina* stock. The radula of *Echininus cumingi* from the Indo-Pacific has a reduced central tooth (fide Troschel, 1858, pl. 11, fig. 7) and enlarged lateral teeth. Among the *Nodilittorina*, our Atlantic *N. tuberculata* Menke has a strongly compressed, elongate central tooth (fig. 57, *b*). The Indo-Pacific *N. pyramidalis* has a much less reduced central tooth which closely resembles that in the members of the subgenus *Melarhaphe*. It may be noted that members of such species as *Littorina* (*Littorina*) *littorea* Linné and *irrorata* Say have a well-developed, almost square central tooth.

The radula ribbon of *Echininus nodulosus* measured 115 mm. in length in one specimen, 110 mm. in another. This is 7 to 8 times the length of the shell. The ribbon is twice the width of that found in a *Nodilittorina tuberculata* Menke of the same shell size. The number of transverse rows is about 1,250. In *N. tuberculata* there were about 1,225 rows, in *Tectarius muricatus* 1,500 rows in a ribbon 67 mm. in length. Pelseneer (Mollusca, Treatise in Zoology, 1906) reports 3,600 rows in *Littorina littorea*. I do not know if there is any phylogenetic or ecological significance to these various number of rows.

Geographical Distribution.—The range of this species is presented in figure 56, *b*, and its restricted distribution is discussed in the remarks under *Nodilittorina tuberculata*. The species is usually abundant where it occurs.

New records.—Florida: Stock Island, Key West (C. I. Aslakson); Indian Key; Fortune Island (P. Bartsch). Bahamas: Nassau, New Providence Island (H. Dodge); South Bight, Andros Island (P. Bartsch); Pimlico Island, Racoon Cay, Ragged Islands (P. Bartsch). Cuba: Cape Cajon; Santa Cruz; Cienfuegos Harbor; Santiago de

Cuba. JAMAICA: Robins Bay, St. Marys; Montego Bay, St. James; Port Henderson; Annotta Bay (all C. R. Orcutt). HISPANIOLA: Morne Rouge, southwestern Haiti; Beata Island (A. Wetmore). PUERTO RICO: Rincon Lighthouse, Mona Passage (G. L. Warmke and N. T. Mattox). VIRGIN ISLANDS: St. Croix (H. F. Dunn). CARIBBEAN ISLANDS: Navassa Island. (All records USNM.)

Phylogenetic position of Echininus.—From the anatomical evidence presented here, it appears that there is little doubt that *Echininus* has many characters that are typically littorinid. This is especially true in the case of the long radula ribbon, the form of the teeth, the presence of an open seminal groove (instead of a closed, internal seminal canal) on the penis, and the simple tentacles with the eye set near the base. We reject Kesteven's (1903) placement of this genus in the family Modulidae. He did so on two characters—the tooth on the base of the columella, and the multispiral operculum. However, Kesteven was in error in stating that members of the genus *Echininus* (*Echinella*, as he called it) have a small tooth at the base of the columella. It is only in the *Tectarius*, sensu stricto, group (with paucispiral opercula) such as *T. coronarius* Lamarck, that we find a basal tooth. This leaves only the multispiral operculum as a character in common with *Modulus*, and although this character may be of convenient generic value in some cases, it certainly is not always a family character.

I believe that the following characters found in *Modulus*, and absent in *Echininus*, exclude the latter from the family Modulidae: Eyes located half way up the length of the tentacles, small digitations along the border of the mantle edge (Abbott, 1944, pl. 1); female with an "ovipositor" organ on the right side of the body; radula relatively short (100 to 150 transverse rows) with a thin, oval, 7-denticled central tooth; a lateral and two marginal teeth which are denticulated (the entire radula closely resembles that in the Rissoacea). Although not necessarily of phylogenetic importance, it may be pointed out that the feces of many, if not all, Littorinidae are relatively short (2 or 3 times as long as wide) and are lined up in the rectum, one directly behind the other, while in *Modulus modulus* Linné the feces are quite long (5 or 6 times as long as wide) and are closely packed side by side at an oblique angle in the rectum, as in the Thiaridae.

In summary of the position of *Echininus*, I am inclined to consider it a specialization of the ancestral stock of the *Melarhaphe* group in the family Littorinidae which has shown a tendency towards the abortion of the central tooth in the radula, an enlargement and closer juxtaposition of the marginals, the reduction of the ditaxic fissure in the foot, a reduction in the size of the osphradium, and the increase

in the number of whorls in the operculum to a degree where it has become multispiral.

It should be pointed out that Kesteven included the genus *Peasiella* Neville in the family Modulidae. Although further anatomical study is needed on this genus, I would be inclined (with the radular and opercular characters presented by Kesteven, 1903, p. 633) to include *Peasiella* in the family Littorinidae and in a higher phylogenetic position than the genus *Echininus*. Kesteven also erected a new family, the Risellidae, for the inclusion of *Risella* Gray (now *Bembicium* Philippi) and *Risellopsis* Kesteven, 1902 (not Cossmann, 1908, which was renamed *Riselloidea* Cossmann, 1909). The new family name, Bembiciidae, was introduced by A. W. B. Powell (1937, p. 67). Before accepting this family, it would be best to have an anatomical study made, and, in the meanwhile, allow it to remain in the family Littorinidae as do J. Thiele and W. Wenz.

Genus *Tectarius* Valenciennes, 1833

Subgenus *Cenchrites* von Martens, 1900

Tectarius muricatus Linné

Tectarius muricatus Linné, Systema naturae, ed. 10, vol. 1, 1758.

Observations on living specimens from Vedado, Habana, Cuba, show that the animal is typically littorinid. The tentacles are one-third longer than the extended proboscis, are cylindrical and tapering, translucent gray in color with faint circular bars of brown. The proboscis is dark brown. The mantle edge is thickened, cream yellow in color, and slightly undulatory. The sides of the foot are light slate-gray with numerous, fine, clusters of chalk-white, embedded granules. Underside of foot is slate gray.

The mode of foot progression is ditaxic with a few simultaneous retrograde waves; that is, the sole of the foot is divided down its length from anterior to posterior by a faint fissure, and each side half acts independently of the other much in the manner of a person shuffling forward with his feet in a potato sack. On each half, a dark wave appears at the anterior end at the same time and moves towards the posterior end (retrograde wave). A bibliography concerning this subject is given by H. W. Lissmann (1945). This same type of progression was reported for *Littorina littorea* Linné (Vlès, 1907; Parker, 1911), *Littorina saxatilis* Olivi (as *L. rudis* Maton), and *Nodilittorina tuberculata* Menke (as *Tectarius nodulosus* from Bermuda) (Parker, 1911).

The penis of *Tectarius muricatus* is the simplest of the littorinids I have examined from the Western Atlantic, and, except for the absence of sawlike frills on one edge, it is not unlike that of *Littorina littorea*

Linné. It is located at the usual position on the right side of the body, and consists of a simple bent, tapering prong which bears a thin, seminal groove along its posterior edge.

The radula in one specimen was 67 mm. in length, with about 1,500 transverse rows of teeth. As in *Littorina*, the unused rows are coiled tightly like a watch spring in a pocket on the dorsal region behind the head. The central tooth is about half as wide as long, not unlike that in *Nodilittorina*, and bears a large central cusp with a smaller cusp on each side. (See fig. 57, *d*.)

The shell is adequately illustrated in Johnsonia by Clench and Abbott (1942).

Geographical distribution.—In addition to the records noted on the accompanying map (fig. 56, *c*) of the West Indian region, I am listing a few new ones which represent either extensions of the range, additional major islands, or the filling in of large gaps (for other records, see Clench and Abbott, 1942). Distribution in the Caribbean region, lower Florida, and Bermuda is almost identical with that of *Nodilittorina*.

New records.—Bahamas: South Bight, Andros Island; Little San Salvador Island. Cuba: Matanzas; Cardenas Bay; Port Gibara; Santiago de Cuba. Hispaniola: Fort Liberte, Dept. du Nord; Cap Haitien, Dept. du Nord; Torbeck and Aquin, Dept. du Sud; Santa Barbara de Samana. Jamaica: Buff Bay, Portland; Stony Cave, St. Mary; Great Pedro Bay, St. Elizabeth; Runaway Bay, St. Ann; Montego Bay, St. James; Morant Bay, St. Thomas; Little Cayman Brac (C. R. Orcutt). Puerto Rico: Mayagüez; Hamacoa. Lesser Antilles: Marigot, Dominica. Caribbean Islands: Curaçao; Aruba. Central America: Utilla Island and Roatan Island, Honduras; Colón, Panamá; Cartagena and Porto Colombia, Colombia; Tucacas, Falcon, Venezuela. (All records USNM.)

References

ABBOTT, R. TUCKER.
1944. The genus *Modulus* in the Western Atlantic. Johnsonia (Harvard Univ.), vol. 1, No. 14, 6 pp., 2 pls.
1949. Sexual dimorphism in Indo-Pacific *Strombus*. Nautilus, vol. 63, No. 2, pp. 58–61, 1 fig.

BEQUAERT, JOSEPH C.
1943. The genus *Littorina* in the Western Atlantic. Johnsonia (Harvard Univ.), vol. 1, No. 7, 27 pp., 7 pls.

CLENCH, WILLIAM J., and ABBOTT, R. TUCKER.
1942. The genera *Tectarius* and *Echininus* in the Western Atlantic. Johnsonia (Harvard Univ.), vol. 1, No. 4, 4 pp., 3 pls.

HABE, TADASHIGE.
1951. Littorinidae in Japan. Illus. Cat. Japanese Shells, vol. 1, No. 4, pp. 87–93, 1 pl.

HEDLEY, CHARLES.
1901. A revision of the types of the marine shells of the Chevert Expedition. Records Australian Mus., vol. 4, p. 121.

KESTEVEN, H. LEIGHTON.
1903. Notes on Prosobranchiata, No. 2—Littorinacea. Proc. Linn. Soc. New South Wales, 1902, pt. 4, pp. 620–636, 1 pl.

LEBOUR, MARIE V.
1945. The eggs and larvae of some prosobranchs from Bermuda. Proc. Zool. Soc. London, vol. 114, pt. 4, pp. 462–489, figs.

LISSMANN, H. W.
1945. The mechanism of locomotion in gastropod molluscs. Journ. Exper. Biol., vol. 21, No. 1, pp. 58–69, 11 figs.

MATTOX, NORMAN T.
1949. Effects of drying on certain marine shells from Puerto Rico. Ecology, vol. 30, No. 2, pp. 242–244, 2 figs.

OSTERGAARD, JENS MATHIAS
1950. Spawning and development of some Hawaiian marine gastropods. Pacific Sci. (Honolulu), vol. 4, No. 2, pp. 75–115, 42 figs.

PARKER, GEORGE H.
1911. The mechanism of locomotion in gastropods. Journ. Morph., vol. 22, pp. 155–170.

POWELL, A. W. B.
1937. The shellfish of New Zealand. 100 pp., 18 pls.

TOKIOKA, T.
1950. Droplets from the plankton net: V, New names for egg capsules of littorinid gastropods. Publ. Seto Marine Biol. Lab., vol. 1, No. 3, pp. 151–152, fig. 6.

TOKIOKA, T., and HABE, TADASHIGE
1953. Droplets from the plankton net: XI, A new type of Littorina-capsula. Publ. Seto Marine Biol. Lab., vol. 3, No. 1, pp. 55–56, fig. 11.

VLÈS, F.
1907. Sur les ondes pédienses des mollusques reptateurs. Compt. Rend. Acad. Sci. Paris, vol. 145, pp. 276–278.

WENZ, WILHELM.
1939. Gastropoda. Handb. Paläozool., vol. 6, pt. 4, pp. 481–720. [See p. 523.]

U. S. GOVERNMENT PRINTING OFFICE: 1954